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THE STRUCTURE AND DEVELOPMENT OF SECOTIUM AGARICOIDES

HENRY S. CONARD

(WITH PLATE 157 AND 1 TEXT FIGURE)

This curious fungus was first found in Ukrain by Czerniaiev in 1845. Specimens from America described by Peck (1882) as *S. Warnei* were examined by Hollós (1903) and pronounced specifically identical with the European plants. This conclusion seems fully justified so far as can be judged by the excellent colored plate and full description given by Czerniaiev. It is therefore a plant of very wide distribution. Hollós records it from Ohio to Wisconsin and Kansas in North America, as well as from Europe, Asia, Africa (Algeria), New Zealand, and Australia (Banks Peninsula).

Secotium agaricoides resembles a puffball in general appearance, being from 4 to 6 or 8 cm. in diameter; but it stands on a short stalk, and the stalk continues through the body of the fungus as a columella. The interior is filled with branched and much folded lamellae instead of a capillitium. Sometimes the body does not dehisce at all; in other cases, it splits lengthwise or the peridium separates slightly from the stalk after the manner of an agaric. The spores are olive-brown in color when seen in mass. They are ovoid in shape and measure $7 \times 5\ \mu$. They have smooth, thick, impervious walls, with one apical germ pore. They are borne in fours on rather long sterigmata, upon clavate basidia, which at maturity are about $22 \times 6\ \mu$. The spore often carries with it a part of the sterigma as an appendage. The present study attempts to throw some light on the nature of this curious plant from the standpoint of development.

My material consisted of about 100 mature plants and 6 small young ones. One 13 mm. and one 15 mm. in diameter were collected in 1911. The others, 10 mm. tall and 8 mm. in diameter, 10 mm. tall and 9 mm. in diameter, 4 mm. tall and 3.8 mm. in diameter, and 4 mm. tall and 3.5 mm. in diameter, were collected in 1912. All were cut open, fixed in chromo-acetic acid, sectioned in paraffin 3⅓, 6⅔, or 10 microns thick, and stained with various stains. The best results were obtained with Haidenhain's iron-alum-haematoxylin. The mature specimens were dry when collected and were stored in boxes.

Development.—The youngest specimens are nearly globular, white, and smooth. Then comes a "button" stage, with the upper portion slightly larger than the stalk and the surface still smooth. Later, the fertile portion increases greatly in height and diameter, leaving the free stalk as a mere basal projection. The superficial brown scales of the peridium appear only when near full maturity. The spores are fully mature while the trama, peridium, and stalk are still fleshy. The old specimens, at least in our climate, dry up and do not putrify.

The Peridium.—Sections of the 3.5 mm. specimen show an indefinite outer layer of loosely woven hyphae surrounding a dense mass of closely packed threads (Pl. 157, fig. 1). Within this globular body and near its summit a ring of deeply-staining tissue is already found. This is the fundament of the hymenophore. In older specimens, the hymenophore hyphae take a distinctly radial and longitudinal direction and form a thick and well-marked zone. Between this layer and the outer webby portion, the hyphae are less crowded and take a paler stain. Their course is predominantly longitudinal (radial). This layer is continuous below with the substance of the stalk. At this stage (9 mm. in diameter), the outer webby layer is more prominent and continues down upon the stalk of the "button." Soon after this, however, the layer completely disappears. The mature peridium shows only a broad layer of longitudinal hyphae, with a thin superficial layer of crushed and withered threads.

The outermost loose layer of the young plant (Pl. 157, fig. 5, 6) agrees in structure and position with the universal veil or blematogen of the evolvate agarics (*Agaricus,* Atkinson 1906, 1914a; *Armillaria,* Atkinson 1914b; and *Stropharia,* Zeller 1914). The second layer forms the bulk of the tissue of the peridium.

The mature peridium is fleshy to leathery in texture. It is about 2 mm. thick on the sides of the body, thinning below to nothing when it breaks away from the stalk, and thickening above to its union with the columella. The scales on its surface are not separate from it, but when caught with forceps and peeled off, the tissue tears deeper and deeper into the peridium. The summit of the columella is continuous with the peridium and of similar structure.

In our 9 mm. specimen, there is a layer of open-meshed "neutral tissue" just within the gleba, surrounding the lower part of the columella. This layer is broadest where the peridium joins the stalk. It probably represents the layer of stem tissue which in *Agaricus campestris* is torn off with the annulus in the expansion of the cap. It appears only in this one specimen. In the 13 mm. specimen, the pileus or peridium joins the stipe by a broad confluence of tissues, representing the undifferentiated partial veil. At the line of junction, the hyphae appear greatly tangled, for the hyphae of the stipe run approximately longitudinally and are continuous with those of the columella, and the prevailing direction in the peridium is meridional. It is doubtless along this tangled region that marginal dehiscence occurs.

The Hymenophore.—The hymenophore appears in the 3 mm. specimen as a horizontal ring of deeply-staining tissue within the globular fungous body and near its summit (Pl. 157, fig. 1). The hyphae composing this ring are rich in protoplasm and very densely tangled together. They do not appear to follow any one direction more than another. Their ends are simply rounded.

In the 3.8 mm. specimen (Pl. 157, fig. 2), this dense ring of hyphae has organized a distinct palisade of round-tipped threads. A median longitudinal section of the carpophore shows this already in two deeply stained lunate areas, concave downward. The tissue beneath these patches is very loose and open, with an occasional lacuna (fig. 4). No sign of gills yet appears in tangential sections (fig. 3). Already, however, the palisade hyphae are swollen at the ends to form basidia and under these basidia the first formation of the gill chamber takes place by a tearing away of the underlying hyphae. The palisade is evidently spreading both centripetally and centrifugally. The centripetal advance encroaches on the stipe for a short time and then ceases. This causes the decurrence of the lamellae, mentioned later. The centrifugal spreading is much more rapid and continues as the "marginal growth of the pileus" until the mature size of the carpophore is reached. The boundary of the pileus is first evident in the upper part of the 3.8 mm. specimen. Thus, the hymenophore distinctly precedes the pileus and the gill chamber in differentiation.

Just how the circle of palisade gives rise to the gill system, my material does not show. My next stage (9 mm., fig. 5, 6) has a ring of well-formed gills extending from the cap toward the columella. The gills are much branched and anastomosing. They run primarily in a radial direction. Near the apex of the body, the gills are united with the columella, or in other words are decurrent (fig. 6, *a*). An older specimen shows the tramal tissue apparently continuous with the columella in many places. This is doubtless the result of a secondary mingling of hyphae, for in mature specimens the gleba is everywhere adherent to the columella, while in the 10 mm. specimen there is a distinct air cavity between the gills and the columella. Growth of the gills is chiefly marginal, though apparently folds may originate and develop at any place. The extension of the gill system as a whole takes place in the region where the peridium joins the stem; corresponding to the marginal or centrifugal extension of agarics (fig. 6, *b*). In this region, the hyphae are narrow, protoplasmic, densely crowded, nearly parallel, and curved downward and inward. They have simple rounded ends. As general growth of the fertile portion of the carpophore goes on, a loosening of the tissues between this growing zone and the stem occurs and into this loose region the hymenophore hyphae constantly penetrate. Quickly the hyphae branch and form a dense hymenium of long, clavate basidia.

The mature gills are much branched and folded. The tramal tissue consists wholly of long, branching, and nearly parallel hyphae, whose ultimate branchlets form the densely crowded basidia. There are no cystidia or other aberrant cells. From a fairly dense web in growing stages, the trama becomes looser toward maturity and finally becomes dry and fragile. From the above account, it is clear that the carpophore of *Secotium agaricoides* presents in its origin and development an exact counterpart of that of *Agaricus* (Atkinson 1906, 1914a). There is at first a universal veil like that of several evolvate agarics (*Agaricus, Armillaria,* and *Stropharia*). There is an ill-differentiated partial veil. The origin of the hymenophore agrees precisely with that of all recently reported agarics, except *Hypholoma* (Allen 1906) and *Coprinus* (Levine 1914). The marginal growth of the gill system is also familiar in the mushrooms. The columella comes into being exactly as does the stipe of mushrooms. Indeed, we might well speak of stipe and pileus of *Secotium,* rather than of peridium and columella. The basidia and spores have the shape, size, and arrangement found in agarics. The copious branching of the gills exceeds anything seen in agarics. The failure of the cap and gills to expand, the drying up of the trama into a friable mass of tissues and spores, the olive-brown color of the spores, and the freedom of the spores to "puff" when the exposed mass is touched, are all lycoperdinean characters.

Histology and Cytology.—The cell structures of *Secotium* present nothing novel. In the sections showing the earliest fundament of the hymenophore, there are in the ring of active growth a few hyphae which are twice as stout as the others; they stain of an even dark color with haematoxylin, without granules of any kind. In the 9 mm. specimen, many hyphae in the stipe, columella, pileus, and trama stain deep-red with safranin. They are of the usual diameter and show no granules. As the stem of this specimen is bored by insect larvae (fig. 6), these may be dead hyphae. They are absent from the region of active growth at the margin of the pileus.

The cells of the mycelium vary from 2 to 10 times as long as wide. The end walls usually show the little central mass of stainable material associated by Strasburger with the pores in the partition (fig. 1, 5). In several instances, the cells of the tramal hyphae had two distinct nuclei. Metachromatic bodies are numerous, especially in the hymenium and regions of active growth. Many paler bodies were seen along the walls of some cells.

The rhizomorph connected with the base of the carpophore in my 3.8 mm. specimen is composed of three kinds of hyphae. (1) Most hyphae are very slender (3.5 microns), homogeneous or slightly granular. They form the fundamental tissue of the entire structure (fig. 1, 11). (2) Among these are groups or strands of larger hyphae (fig. 1, 11), and occasionally very large ones (10 microns). These show distinct nuclei, certain globular bodies, and numerous square crystals (fig. 1, 13). As the crystals stain deeply, they are probably of protein, as found by van Bambeke in *Lepiota meleagris*. The course of these larger hyphae is mostly longitudinal, but they are much tangled. They are not found in the carpophore. (3) On the surface of the rhizomorph, are many slender (2.5 to 3 microns) hyphae with very thick walls (1 micron, fig. 1, 12); in places they form a rather compact layer, but they occasionally extend into the center of the rhizomorph. The walls stain both with haematoxylin and eosin; no contents were observed.

The young basidium possesses two nuclei near the middle of the cell (fig. 1, 12), usually lying in the longitudinal axis of the cell. These nuclei, like those of the mycelium generally, are small, sharply outlined, with one large nucleolus and little or no other visible substance. Later a single large nucleus of similar structure is found near the distal end of the basidium (fig. 1, 6, 8). Although satisfactory fusion stages were not found (fig. 1, 3, 4), there is doubtless a fusion of nuclei to form this one large nucleus. Still later, two (fig. 1, 7) and then four nuclei are found, clustered about the apex of the basidium (fig. 1, 8). The mitoses were not observed. The four sterigmata then grow out symmetrically and a spore forms on each (fig. 1, 9, 10). The entrance of the nuclei into the spores was not observed, but some of the spores were clearly seen to possess a single nucleus.

So far as observed, then, the cytology of *Secotium* agrees with that of other hymenomycetes.

Discussion.—What of the relationships in general? Fischer (1899) in the Pflanzenfamilien admits "about twenty species" of *Secotium*, including the genera *Endoptychum* Czern. and *Elasmomyces* Cav. The gill structures of *S. erythrocephalum* Tul. and *S. Mattirolianus* (Cav.) agree well with those of *S. agaricoides* (Czern.), but Cavara (1897) describes a large-celled pseudoparenchyma in the stipe and peridium of his species. This tissue occurs in layers alternating with layers of hyphal tissue. The spores, also, of *S. Mattirolianus* are rough, roundish, and of two sizes. Cystidia occur in Cavara's species, as also according to

Corda (1854) in *S. Gueinzii* Kunze. No cysts are described by Corda for *S. melanosporum* Berk. or *S. coarotatum* Berk. If, therefore, Fischer has done well in uniting *Endoptychum* and *Elasmomyces* with *Secotium,* we must recognize two or perhaps three well marked subgenera. The other species of *Secotium* are not well enough known to admit of discussion.

Regarding the other genera united with *Secotium* by Fischer (1899) in his Secotiaceae, *Polyplocium,* as Fischer himself notes, is nearer to *Boletinus* than it is to *Secotium. Gyrophragmium* may prove to be near to *Secotium,* but Fischer regards it as close to *Montagnites* and *Coprinus,* to which *Secotium* is certainly not closely allied. As to *MacOwenites* and *Cauloglossum,* too little is known of them, but they do not seem to resemble *Secotium* so closely as the latter resembles *Agaricus.*

The Hysterangiaceae and Hymenogastraceae which make up the rest of the Hymenogastrineae of Fischer are each fairly homogeneous in themselves. They relate quite distinctly to the Clathraceae, Lycoperdacaeae, and Nidulariaceae. They resemble Secotiaceae only in the fact that their spores mature while the hymenophore is still fleshy. But this is equally true of Agaricaceae. There remains therefore no real unity in Fischer's Hymenogastrineae and that author's opinion seems strengthened that the Secotiaceae, at least should be dismembered and its genera distributed among the Hymenomycetes.

Fischer (1900) and Lotsy (1907) have considered *Secotium* as a possible point of departure for the Phallaceae. Lotsy refers directly to the little known *S. olbium.* The argument is based on the manner of development of the hymenophore. Further, Corda's figure of *S. Gueinzii* (Pl. 6, fig. 12) shows trabeculae running through the gleba from the top of the stipe to the peridium, after the manner of a young clathroid, but Corda's section cannot be median, as it shows no columella; and it throws no light on the origin of the hymenophore. We have seen that in respect to development *S. agaricoides* is precisely like *Agaricus campestris* and *A. arvensis* as described by Atkinson (1906, 1914a). It is not like *Phallus* or *Mutinus,* nor can the stipe and columella of *Secotium* be likened to the stalk of a phalloid; for the phalloid stem probably represents a sterilized gleba, and is therefore comparable with the sterile base of a *Lycoperdon*. But the columella of *Secotium agaricoides* is in its origin, development, and structure strictly agaricinean. There would seem to be no support whatever for relating our plant to the Phallaceae. The likeness of *Secotium* to a puffball as noted on a previous page, though quite real, is decidedly superficial, and cannot carry much weight.

On the whole, *S. agaricoides* would best be placed near to *Agaricus* (*Psalliota*), either in the Agariceae or Marasmiae of Hennings (1897). It clearly falls within the Agaricaceae of Maire (1902). It is to be regarded as a primitive or arrested agaric,—perhaps a paedogenic form, reaching its reproductive maturity in the "button" stage.

SUMMARY

1. *Secotium agaricoides* is a widespread species, occurring in Europe, Asia, Africa, North America, Australia, and New Zealand.

2. In the young carpophore, the fundament of the hymenophore first appears, followed by the demarcation of the margin of the pileus and the appearance of a gill cavity.

3. The development of the "peridium" is like that of the cap of *Agaricus campestris,* showing a primitive *velum universale* and a pileus. No true *velum partiale* is found, though a layer of "neutral tissue" occurs which may represent it. The universal veil disappears during the maturation of the plant.

4. The hymenophore consists of radiating, branched, and anastomosing gills decurrent at the top of the columella.

5. The trama and hymenium are simple in structure, without pseudoparenchyma or cystidia.

6. The young basidium has two nuclei, which unite to form one. This latter divides twice to form four nuclei for the four spores. The mycelial cells are binucleate.

7. *Secotium agaricoides* is nearly related to *Agaricus* (*Psalliota*), being an arrested or paedogenic form. It is not closely related to the Gasteromycetes or Phalloids.

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GRINNELL, IOWA.

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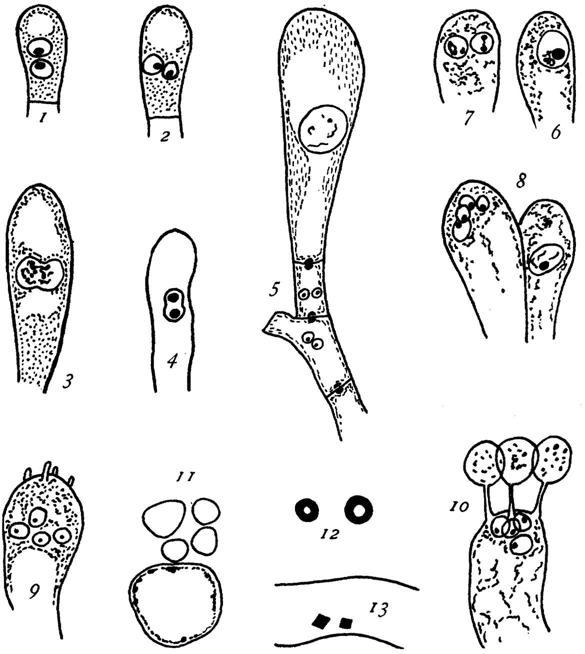


FIG. 1. 1, 2, young binucleate basidia. 3, 4, fusion of nuclei in young basidium. 5, uninucleate basidium, with cells of subhymenium. 6, fusion-nucleus of basidium, probably in synapsis. 7, two nuclei resulting from division of fusion-nucleus. 8, basidium on right with fusion-nucleus; on left 4-nucleate stage. 9, budding out of sterigmata. 10, formation of basidiospores. 11, central hyphae of rhizomorph in cross section; two sizes with intercellular spaces. 12, thick walled hyphae from surface of rhizomorph. 13, protein crystals in large hyphae of rhizomorph. All drawings made with camera lucida; 1, 2, 3, 4, 5, 11, 12, 13 with $\frac{1}{6}$ in. objective; 6, 7, 8, 9, 10, with $\frac{1}{12}$ in. objective.

DESCRIPTION OF PLATE CLVII

Photomicrographs by Paul H. Smith

Fig. 1. Median longitudinal section of specimen 3.5 mm. in diameter. First indications of pileus and hymenophore.

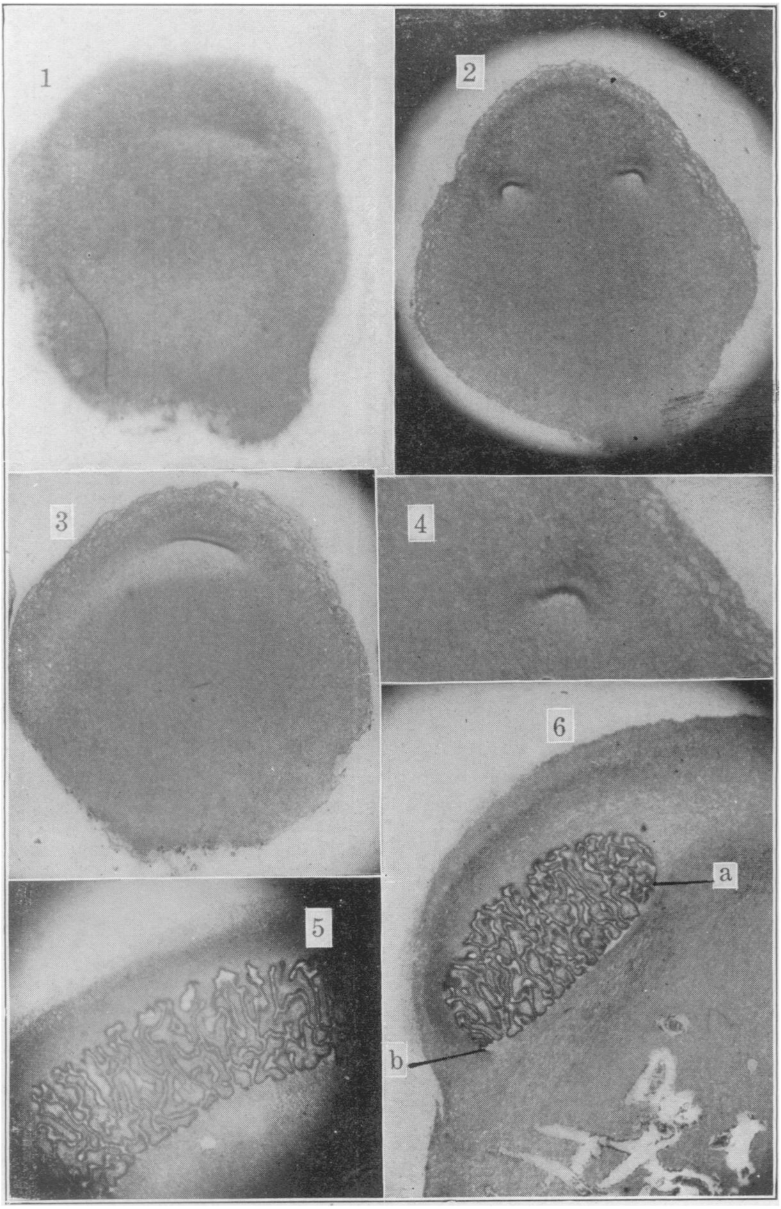
Fig. 2. Median longitudinal section of 3.8 mm. specimen. Fundament of hymenophore and gill chamber.

Fig. 3. Tangential section of same specimen.

Fig. 4. Portion of Fig. 2, enlarged.

Fig. 5. Transverse section of 9 mm. specimen.

Fig. 6. Median longitudinal section of 9 mm. specimen. a, decurrence of gills; b, marginal growth of gills.



SECOTIUM AGARICOIDES (CZERN.) HOLLÓS